Simulating the effects of climatic variation on stem carbon accumulation of a ponderosa pine stand: comparison with annual growth increment data

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Summary

Simulation models of ecosystem processes may be necessary to separate the long-term effects of climate change on forest productivity from the effects of year-to-year variations in climate. The objective of this study was to compare simulated annual stem growth with measured annual stem growth from 1930 to 1982 for a uniform stand of ponderosa pine (*Pinus ponderosa* Dougl.) in Montana, USA. The model, FOREST-BGC, was used to simulate growth assuming leaf area index (LAI) was either constant or increasing. The measured stem annual growth increased exponentially over time; the differences between the simulated and measured stem carbon accumulations were not large. Growth trends were removed from both the measured and simulated annual increments of stem carbon to enhance the year-to-year variations in growth resulting from climate. The detrended increments from the increasing LAI simulation fit the detrended increments of the stand data over time with an R^2 of 0.47; the R^2 increased to 0.65 when the previous year's simulated detrended increment was included with the current year's simulated increment to account for autocorrelation. Stepwise multiple linear regression of the detrended increments of the stand data versus monthly meteorological variables had an R^2 of 0.37, and the R^2 increased to 0.47 when the previous year's meterological data were included to account for autocorrelation. Thus, FOREST-BGC was more sensitive to the effects of year-to-year climate variation on annual stem growth than were multiple linear regression models.

Introduction

Predictions of forest response to global climate change require process models of ecosystems that are sensitive to the year-to-year variations in climate represented in the annual growth rings of trees. In dendrochronology, indices of annual tree-ring increments are related to climatic variables by multiple linear regression (Fritts 1976, Cook and Kairiukstis 1990). Ecosystem processes, such as evapotranspiration, are not usually better predictors of tree-ring indices than monthly climatic data in dendrochronological models (Federer et al. 1989, Serre-Bachet and Tessier 1990, however, see Cook and Jacoby 1977).

FOREST-BGC is a forest ecosystem process model that simulates the carbon, nitrogen and hydrologic biogeochemical cycles for a homogeneous forested area (Running and Coughlan 1988, Running and Gower 1991). Output of model simulations for single years have been compared with wood production and hydrologic data (McLeod and Running 1988, Nemani and Running 1989). Furthermore, single-year simulations of net primary productivity agreed with remotely sensed data over a wide range of climates, from Florida to Alaska, showing that FOREST-BGC is sensitive to extreme differences in climate (Running and Nemani 1988). However, FOREST-BGC has not been tested for long-term carbon balance or sensitivity to climatic

variation at a single site.

A major test of a model's ability to predict ecosytem response to future climate change is its ability to predict responses to recent past variations of climate. The first objective of this study was to compare predictions of stem growth over time using FOREST-BGC with stem analysis data for a uniform stand of ponderosa pine (Martin 1987, McLeod and Running 1988). The resulting coefficient of determination (R^2) of the above comparision cannot be interpreted without some reasonable criterion. Thus, the second objective of this study was to compare the predictive ability of FOREST-BGC with that of multiple linear regression models, using the same climatic and stem analysis data.

It is well known that there is a significant amount of autocorrelation between the previous year's and the current year's growth rings (Fritts 1976, Cook and Kairiukstis 1990). Linder et al. (1987) showed that needle length of *Pinus radiata* D. Don. is a function of water stress during the period of extension, providing a physiological basis for the autocorrelation. Thus, the predictive ability of FOREST-BGC and multiple linear regression models were compared with and without accounting for the previous year's annual growth.

Model description

FOREST-BGC (for BioGeochemical Cycles) has two time steps: daily for simulation of the hydrologic cycle, net photosynthesis and maintenance respiration; and yearly for the simulation of the remainder of the carbon cycle and the nitrogen cycle (Running and Coughlan 1988, Running and Gower 1991). For the objectives of this study, we simulated only the hydrologic and carbon cycles, and not the nitrogen cycle, and we did not use the dynamic carbon partitioning of Running and Gower (1991).

The model requires readily available daily meteorological data (Table 1). The mountain-climate simulator program, MT-CLIM (Running et al. 1987), is used to extrapolate the weather station data to total daily solar radiation, minimum and maximum air temperatures, dew point temperature, soil temperature, and daily precipitation at the site. Precipitation is either intercepted by the canopy and evaporated, or routed to the soil water compartment. Excess soil water above field capacity is removed as runoff. Transpiration is calculated using a Penman-Monteith equation, for which stomatal conductance is a complex function of maximum stomatal conductance, air and soil temperatures, vapor pressure deficit, daily solar radiation, and predawn soil/leaf water potential. Incident radiation is attenuated through the canopy according to Beer's law to get an average canopy absorbed radiation. Daily net photosynthesis is calculated by multiplying the CO_2 concentration gradient (assumed to be the atmospheric CO_2 concentration minus the CO_2 compensation point) by canopy conductance (from the Penman-Monteith equation) in series with a mesophyll conductance. Mesophyll conductance is determined from the maximum photosynthetic rate, air temperature, and average canopy absorbed radiation. Daily maintenance respiration is sum of the 24-hour stem and root respiration and the

Table 1. FOREST-BGC driving, site, and output variables and physiological parameters (Running and Coughlan 1988).

Variable or parameter	Units
Required daily inputs	
Day of year	
Air temperature, maximum	°C
Air temperature, minimum	°C
Precipitation (water equivalent)	cm
Calculated and optional inputs	
Daylength	s
Total solar radiation	$kJ\,m^{-2}\,day^{-1}$
Total photosynthetically active radiation	$kJ\,m^{-2}\,day^{-1}$
Dew point temperature	°C
Soil temperature (20-cm depth)	°C
Atmospheric CO_2	ppm
Site variables	
Latitude	°
Slope and aspect	°
Elevation	m
Albedo	%
Soil water content at field capacity	$m^3\,ha^{-1}$
Soil water content at -1.5 MPa	$m^3\,ha^{-1}$
Initial water: soil, snowpack	$m^3\,ha^{-1}$
Daily outputs	
Water fluxes: transpiration, evaporation, runoff	$m^3\,ha^{-1}\,day^{-1}$
Soil water content	$m^3\,ha^{-1}$
Predawn leaf/soil water potential	MPa
Daily net photosynthesis	$kg\,ha^{-1}\,day^{-1}$
Daily maintenance respiration	$kg\,ha^{-1}\,day^{-1}$
Annual outputs	
Carbon increments: leaf, stem, root, soil, litter	$kg\,ha^{-1}\,year^{-1}$
Total growth respiration	$kg\,ha^{-1}\,year^{-1}$
Major physiological parameters	
Leaf area index (LAI)	dimensionless
Specific leaf area	$m^2\,kg^{-1}$ carbon
Fraction of carbon in dry matter	$kg\,kg^{-1}$
Maximum stomatal conductance	$mm\,s^{-1}$
Boundary layer conductance	$mm\,s^{-1}$
Maximum photosynthetic rate	$\mu mol\,m^{-2}\,s^{-1}$
CO_2 compensation point	ppm
Critical soil/leaf water potential	MPa
Q_{10} for maintenance respiration	
Maintenance respiration: leaf, stem, root	$kg\,kg^{-1}\,day^{-1}$
Growth respiration: leaf, stem, root	$kg\,kg^{-1}\,year^{-1}$
Carbon allocation: leaf, stem, root	%
Precipitation interception coefficient	$mm\,LAI^{-1}$
Light extinction coefficient	LAI^{-1}
Leaf turnover coefficient	$\%\,year^{-1}$
Stem turnover coefficient	$\%\,year^{-1}$
Fine root turnover coefficient	$\%\,year^{-1}$
Initial carbon: leaf, stem, root, soil, litter	$kg\,ha^{-1}$

nighttime leaf respiration; respiration is a function of air temperature with a Q_{10} of 2.0; the respiration coefficients are the maintenance respiration rates at 0 °C.

The total carbon accumulated over the year was then allocated to stems, leaves and roots with a fixed percentage of the total (Table 1). Carbon lost to growth respiration was then removed from total carbon allocated to leaves, stems and roots. Carbon fluxes to the litter are from the fine root and leaf turnover coefficients; the leaf turnover coefficient was set so that carbon lost by turnover was equal to net carbon allocated to the leaves (corrected for leaf growth respiration) necessary to maintain the chosen LAI.

Materials and methods

Site and stand description

Stem volume accumulation in an 83-year-old, even-aged, second-growth stand of ponderosa pine (*Pinus ponderosa* Dougl.) located near Superior, Montana, USA, provided the growth data against which FOREST-BGC and multiple linear regression equations were compared. This stand was carefully selected for uniform site productivity, homogeneous density and limited past mortality (Martin 1987). On two 0.04-ha plots, annual diameter increment was measured on two cores taken at a height of 1.3 m from each tree, and annual height increment was estimated from a multiple regression equation developed from 36 trees within the stand destructively sampled for stem analysis (Martin 1987). Annual increment of stem volume was determined on each of the two plots from the height and diameter measurements and averaged. Annual increment of stem carbon was then calculated from annual volume increment assuming a dry wood density of 500 kg m^{-3} and a carbon content of 45%. Analysis of dead trees in the stand showed that total mortality was less than 0.8% of the total wood volume. Dead tree characteristics and living tree cores suggested that mortality was widely distributed through time and did not substantially influence trends in volume growth (Martin 1987).

In a companion study, water holding capacity of the soil (128 mm) was determined from undisturbed soil samples (McLeod and Running 1988). Total leaf area index (LAI, 5.1) was determined from sapwood area using a regression equation developed from harvested trees, that included samples from this stand (McLeod and Running 1988). The daily minimum and maximum temperatures and precipitation for the years 1930 to 1982 were obtained for the National Weather Service station at Superior, Montana from EarthInfo, Inc. (Boulder, Colorado, USA).

Simulations

We chose some of the FOREST-BGC parameters listed in Table 1 to be more compatible with ponderosa pine. Maximum stomatal conductance and maximum photosynthetic rate were set at 1 mm s^{-1} and 4.0 µmol m^{-2} s^{-1}, respectively (Helms 1972, Hunt et al. unpublished data). Maintenance respiration rate at 0 °C was obtained from Ryan's (1990) data for *Pinus contorta* Dougl. and from Johnson-Flan-

agan and Owen's (1986) data for *Picea glauca* (Moench) Voss for stems and roots, respectively. Allocation of carbon to leaves, stems and roots was set to be 20%, 25% and 55%, respectively (Cannell 1989, Santantonio 1989), and fine root turnover was set at 75% based on data for *Pseudotsuga menziesii* (Mirb.) Franco (Santantonio and Hermann 1985).

Because LAI was not known in 1930 and LAI is a critical parameter to FOREST-BGC (Table 1, Running and Coughlan 1988), we used two different scenarios in the simulations. For the first scenario, we assumed that LAI would be constant after the stand reached an age of 30 years (Waring and Schlesinger 1985) and used the measured LAI of 5.1 from 1930 to 1982. For the second scenario, we estimated an initial LAI from the tree diameters in 1930 using an allometric equation for ponderosa pine relating tree diameter with sapwood area at a height of 1.3 m (R. H. Waring, personal communication). The equation was: $S = (-0.27 + 0.835\ d)^2$, where S is the sapwood area in cm^2, d is the diameter at 1.3 m. The number of samples was 79 trees from 6.1 cm to 33.7 cm in diameter, and the coefficient of determination (R^2) was 0.97. Then to obtain LAI, S (cm^2) was multipled by 0.25 to give projected leaf area (m^2) (Waring and Schlesinger 1985, McLeod and Running 1988); a factor of 2.3 was used to convert projected leaf area to total leaf area; and the density of trees in 1930 was assumed to be 941 ha^{-1}, which was the density in 1983. The resulting LAI for the stand was 2.0. Because the stand reached the culmulation of periodic annual increment about the time of sampling (Martin 1987), we increased LAI exponentially each year from 2.0 in 1930 to the measured 5.1 in 1983. For both scenarios, we started the 53-year simulation using the assumed LAI, the stem carbon mass in 1930 estimated from the stem volume data, and we assumed that root carbon mass was 12.5% of stem carbon mass.

Removal of growth trends

Both the measured and simulated annual increments of stem carbon had growth trends over time that obscured the year-to-year variation of growth resulting from climatic variability. Because the stand was growing exponentially (Figure 1), the derivative with respect to time (annual increment) will be proportional to the current amount (total stem carbon). Thus, we determined the linear regression equation for measured increment of stem carbon with total stem carbon (Figure 2). Subtracting the observed increment from the expected increment resulting from the growth trend, we obtained the detrended increments of stem carbon, which were used in further analyses.

Similarly, we fitted a linear regression equation of the simulated annual increments of stem carbon with respect to total stem carbon for the increasing LAI scenario. We then subtracted the simulated increment from the expected increment resulting from the growth trend to obtain the simulated detrended increments of stem carbon (Figure 3). Thus, the simulated and actual detrended increments were determined in the same manner.
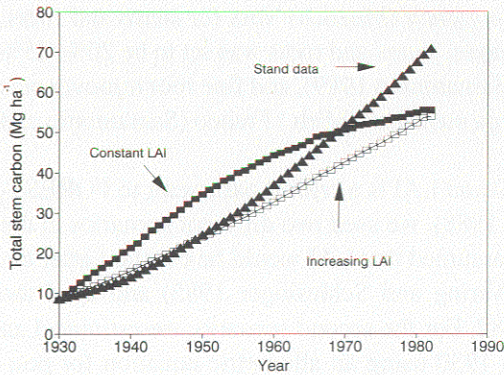
Figure 1. Measured total accumulation of stem carbon for a ponderosa pine stand (▲) and simulated accumulation of stem carbon assuming either constant LAI (■) of 5.1 or increasing LAI (□) from 2.0 to 5.1, because LAI was not known until 1982.
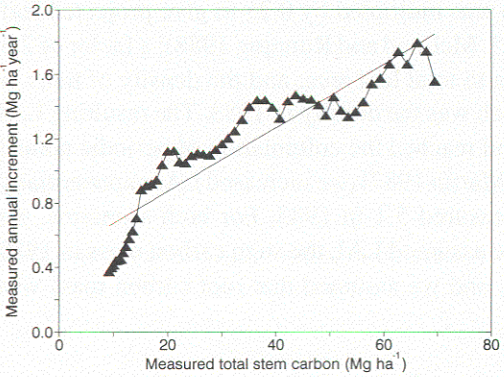

Figure 2. Removal of the growth trend in the data for the ponderosa pine stand. Detrended increments were calculated from the measured annual increment of stem carbon (▲) minus the expected trend resulting from exponential growth (line).
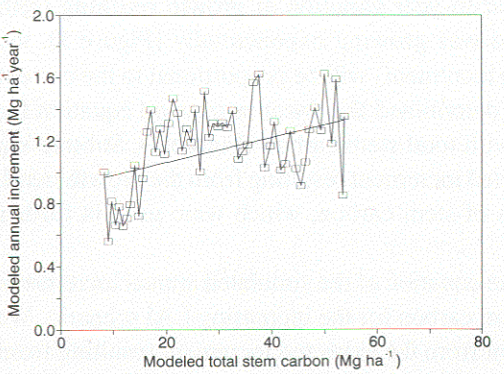

Figure 3. Removal of the growth trend in the 53-year simulation. Detrended increments were calculated from the simulated annual increment of stem carbon (□) minus the expected trend (line) resulting from an exponential increase of LAI from 2.0 to 5.1.

Regression analyses

To evaluate the year-to-year variation of the actual detrended increments of stem carbon using statistical techniques, we obtained the monthly mean climatic data for each year, from 1930 to 1982, using the MT-CLIM extrapolations. We used the stepwise multiple linear regression routine from SAS (version 6.03, SAS Institute, Inc., Cary, North Carolina, USA). The level of significance for inclusion of a variable was set so that the partial F-ratio was 7.0, because the number of observations was about equal to the number of variables which could be included.

To determine the amount of variation of the actual detrended increments of stem carbon that can be explained by FOREST-BGC, we regressed the actual detrended increments (as the independent variable) versus the simulated detrended increments for 53 years. To account for the autocorrelation, we regressed the actual detrended increments versus the previous year's and the current year's simulated detrended increments for 52 years.

Results and discussion

Simulated and measured total stem carbon accumulation

The differences between the simulated and measured accumulations of stem carbon were not large, the maximum error assuming constant LAI was 52% at year 1943 and the maximum error with increasing LAI was 22% at year 1982 (Figure 1). The simulations of stem carbon accumulation were quite different between the two LAI scenarios. In the constant LAI scenario, total photosynthesis was about the same year after year, and the annual maintenance respiration increased as a result of an increase in stem and root mass. Thus, the net carbon available for stem growth became smaller over time, which may be reasonable for an old-growth stand. In the exponentially increasing LAI scenario, total photosynthesis increased allowing for exponential growth (Figure 1).

The different simulated growth trends show the sensitivity of FOREST-BGC to LAI; this sensitivity to LAI was explicitly designed into the model (Running and Coughlan 1988). The simulations for both LAI scenarios may have differed from the measured carbon accumulation because we used constants instead of variables for key parameters such as root turnover and allocation of carbon above and below ground (Running and Gower 1991). The fraction of carbon allocated below ground and fine root turnover rate are among the most sensitive variables for the simulation of wood production and are among the most critical unknowns necessary to balance the carbon cycle for forest ecosystems (Landsberg et al. 1991).

We can obtain a much better fit to the data by adjusting various parameters such as allocation, turnover or maintenance respiration. Indeed, if we increase the allocation of carbon to the stems from 25% to 30% (with a 5% decrease in carbon allocation to the roots), we would almost match the measured accumulation of stem carbon (Figure 1). But changing parameters *a posteriori* would be meaningless because we do not know how LAI varied over the 53-year period. However, our results using

constant parameters, derived from published experimental studies, suggest that the overall carbon budget for forest stands can be balanced using ecosystem simulation models. In the future, we will test the dynamic version of FOREST-BGC (Running and Gower 1991) using these stand data (Figure 1).

Effects of climatic variability

The detrended increments of stem carbon accumulation (Figure 3) explained 47% of the variation of the actual detrended increments from Figure 2 with climate (data not shown). There was a significant autocorrelation between the current year's simulated detrended increments and previous year's simulated detrended increments; the R^2 increased to 0.65 when the previous year's simulated detrended increment was included using multiple linear regression (Figure 4).

The simulated increments show the same trend with time as did the actual increments with noticeable growth reductions during the warm dry 1930's and growth enhancements during the cool moist 1940's and 1950's (Figure 4). Some general circulation models (GCM's) predict that a doubling of atmospheric CO_2 will cause warmer dryer conditions in the northern mid-latitudes (Mitchell 1989), which may be similar to the climate differences between the 1930's and 1940's. To what extent increasing CO_2 will ameliorate an expected reduction in forest productivity from a warmer dryer climate is not fully known (Eamus and Jarvis 1989).

The constant LAI scenario had a different growth trend (Figure 1), in which the annual increment was proportional to the logarithm of total stem carbon (data not shown). The difference between the simulated increments and the log-linear regression were not very different from the simulation detrended increments from the increasing LAI scenario in Figure 3. Therefore, LAI affected the overall trend of simulated stem growth, but not the year-to-year variability resulting from climate.

Stepwise multiple linear regressions explained less of the year-to-year variation of detrended data than did the forest ecosystem process model, both with and without
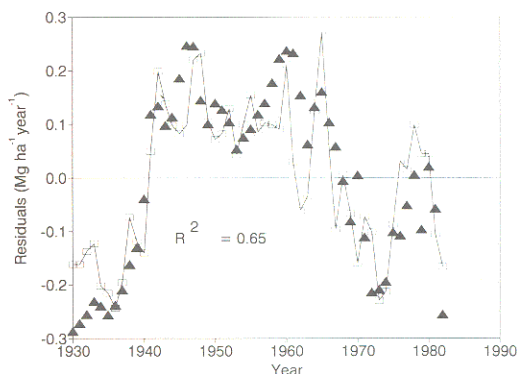

Figure 4. Comparison of actual detrended increments of stem carbon (▲, from Figure 2) with simulated detrended increments (□). The simulated detrended increments combine both the current year's and the previous year's simulated growth increment using multiple linear regression to account for autocorrelation.

the autocorrelation with the previous year's data (Table 2). Since we did not use the sophisticated statistical techniques of dendrochronology (Fritts 1976, Cook and Kairiukstis 1990), these results do not indicate that ecosystem process models are better than dendrochronological models. Moreover, one of the major goals of dendrochronology is to determine past climates from tree-ring indices, a goal that process models cannot accomplish.

The variables selected from monthly meteorological data (Table 2) are related to the year-to-year variation in the length of midsummer drought. Figure 5 shows simulations for two years: 1930 when total precipitation was 339 mm, about one standard deviation lower than the annual mean of 427 mm; and 1965 when total precipitation was 549 mm, about one standard deviation higher than the mean. High radiation in May should increase the rate of soil drying by evapotranspiration leading to an earlier midsummer drought. Precipitation in June and October determine the length of the drought; the length of the midsummer drought is reflected in the greater total net carbon accumulation for the wet year (Figure 5). The higher R^2 with the previous year's June precipitation indicates that the midsummer drought from the previous year affects the current year's growth (Table 2) as found by Linder et al. (1987).

Conclusions

The higher R^2's obtained using FOREST-BGC (Figure 3) compared to regression models (Table 2) indicate that ecosystem process models can better integrate the effects of climate on stem carbon gain than multiple linear regression models. One of the advantages of using FOREST-BGC for predicting annual stem carbon increments is that the simulations are at the same spatial scale (a homogenous forested area) and at the same temporal scale (yearly allocation and growth) as the stand data

Table 2. Fit of the stem analysis residuals to mean monthly climatic data from MT-CLIM for 1930 to 1982.

Regression variable		Partial r	F-ratio	Significance
Current	Intercept	6.96	0.0111	
	May radiation[1]	−0.43	13.06	0.0007
	June precipitation[1]	0.34	9.36	0.0036
	October precipitation	0.30	7.83	0.0074
	Overall R^2	0.37	9.50	0.0001
Current +	Intercept	3.24	0.0781	
previous	May radiation	−0.43	12.07	0.0011
	June precipitation	0.32	9.92	0.0028
	Previous June precipitation	0.32	9.24	0.0030
	October precipitation	0.28	8.87	0.0046
	Overall R^2	0.47	10.37	0.0001

[1] Radiation is mean daily total shortwave radiation (kJ m^{-2} day^{-1}) and precipitation is total monthly precipitation (mm liquid water).
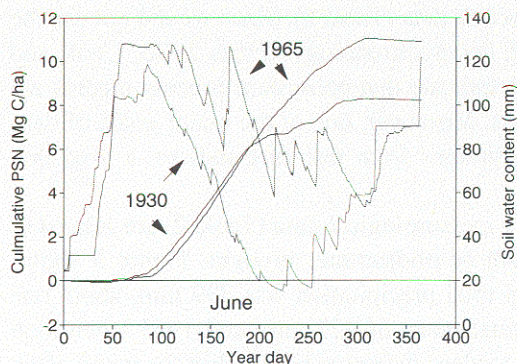
Figure 5. Comparison of culmulative net carbon gain (left axis, solid lines) and soil water content (right axis, dotted lines) for a dry year (1930, 339 mm precipitation) and a wet year (1965, 549 mm precipitation). Daily net carbon gain is the difference between net photosynthesis and total maintenance respiration.

used to verify model simulations. Yet, there is insufficient *a priori* knowledge about changes of LAI over the simulation period and model parameters to come within 10% of the actual carbon accumulation. It may be unlikely that finer spatial and temporal resolution models will do better at these large spatial and yearly temporal scales because of the larger number of parameters that need to be estimated from experimental data.

Acknowledgments

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